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Zangerlia ukhaachelys, New Species, a Nanhsiungchelyid Turtle from the Late Cretaceous of Ukhaa Tolgod, Mongolia

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ABSTRACT

The Late Cretaceous continental deposits of Ukhaa Tolgod, Mongolia, have yielded remains of a new NANHSIUNGCHELYID turtle, *Zangerlia ukhaachelys*, n.sp. This taxon is based on a single individual that consists of a partial cranium, representatives of all peripherals, an almost complete plastron, and limb fragments. *Zangerlia ukhaachelys* is diagnosed as a new taxon by the presence of an anteromedial process of the hyoplastron that reduces the typical contact of the entoplastron with the epiplastron. Phylogenetic analysis firmly places *Zangerlia ukhaachelys* as sister to *Zangerlia testudinimorpha* and *Zangerlia neimongolensis* within NANHSIUNGCHELYIDAE and confirms the close phylogenetic relationships between *Nanhsiungchelys wuchingensis* and *Anomalochelys angulata* and among all North American representatives of *Basilemys*. In addition, there is modest support that all Asian representatives of NANHSIUNGCHELYIDAE form a monophyletic clade, which is primarily diagnosed by a deep, triangular nuchal notch. From a biogeographic standpoint, it is evident that the Late Cretaceous faunas of Asia and North America are closely related; however, phylogenetic considerations demonstrate that faunal exchange was limited for the NANHSIUNGCHELYIDAE.

INTRODUCTION

Central Asian continental deposits have yielded a diverse fauna of Late Cretaceous turtles that are closely related to those from the Late Cretaceous of North America. Asian faunas are characterized by representatives of the ADOCIDAE, CARETTOCHELYIDAE, Lindholmemydidae, NANHSIUNGCHELYIDAE, Macro-

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baenidae, Mongolochelyidae, and TRIONYCHIDAE and contain both aquatic and terrestrial forms (Sukhanov, 2000). Together with faunas from the Late Cretaceous of North America, these groups are of special importance to the systematics of turtles, as they may have given rise to many living cryptodiran groups. As basal relationships of crown CRYPTODIRA are still under debate, a better understanding of the morphology of these turtles may be crucial to resolving patterns of CRYPTODIRE evolution.

Late Cretaceous deposits at Ukhaa Tolgod have produced thousands of vertebrate fossils (Dashzeveg et al., 1995), many of which have been exquisitely preserved. Interestingly, despite the great abundance of fossil mammals, lizards, and dinosaurs, only a few turtles have been discovered to date. During the 1993 joint expedition of the Mongolian Academy of Sciences and the American Museum of Natural History, a partial skeleton of a fossil turtle was uncovered from this locality and preliminarily identified as *Basilemys*? (Dashzeveg et al., 1995). The purpose of this paper is to formally describe this specimen as a new species of NANHSIUNGCHELYIDAE and to explore phylogenetic relationships within this clade of turtles.

INSTITUTIONAL ABBREVIATIONS: **IGM,** Institute of Geology, Mongolia, Ulannbaatar Mongolia; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **YPM,** Yale Peabody Museum, New Haven, CT.

TERMINOLOGY: Anatomical terms of the cranium follow those summarized by Gaffney (1972) and those of the shell as recommended by Zangerl (1969). However, the anterior two pairs of plastral scutes are termed ''gulars'' and ''extragulars'' to clearly distinguish them from the similarly situated, but ostensibly nonhomologous, ''gulars'' and ''intergulars'' of other turtles (Hutchison and Bramble, 1981). Because the generic assignment of most NANHSIUNGCHELYIDS has varied substantially over the last two decades (e.g., Sukhanov and Narmandakh, 1977; Meylan and Gaffney, 1989; Brinkman and Peng, 1996; Sukhanov, 2000; Hirayama et al., 2001), we use the assignments used by Hirayama et al. (2001). Wherever possible, taxa that are more inclusive are referred to with phylogenetically defined clade names as presented by Joyce et al. (2004) and herein (see below). These names are distinguished from traditional rank-based taxonomic names by the small capitals type style throughout the text.

MATERIALS

Several turtle specimens were used for comparative purposes and were integrated into a phylogenetic analysis. These include: *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865), as described by Marsh (1890), Hay (1908), White (1972), and personal observation (WGJ) of YPM 782, holotype of *A. punctatus* Marsh, 1890; *Adocus* sp., as described by Meylan and Gaffney (1989); *Zangerlia testudinimorpha* Mlynarski, 1972, as described by Mlynarski (1972); *Zangerlia neimongolensis* Brinkman and Peng, 1996, as described by Brinkman and Peng (1996) and personal observation (WGJ) of casts of IVPP 020788–7, holotype of *Z. neimongolensis*; ''*Basilemys*'' *orientalis* Sukhanov and Narmandakh, 1977, as described by Sukhanov and Narmandakh (1977) and coded by Hirayama et al. (2001); *Anomalochelys angulata* Hirayama et al., 2001, as described by Hirayama et al. (2001); *Nanhsiungchelys wuchingensis* Yeh, 1966, as described by Yeh (1966) and coded by Hirayama et al. (2001); *Basilemys* (orig. *Compsemys*) *variolosa* Cope, 1876, carapace and plastron as described and depicted by Langston (1956), cranial and other nonshell characters as scored by Hirayama et al. (2001); *Basilemys nobilis* Hay, 1911, carapace and plastron as described and depicted by Langston (1956), postcranial characters as scored by Hirayama et al. (2001); *Basilemys sinuosa* Riggs, 1906, as described and depicted by Riggs (1906); *Basilemys praeclara* Hay, 1911, as described by Brinkman and Nicholls (1993); and *Basilemys* sp., as described by Brinkman (1998).

METHODS

The phylogenetic review of NANHSIUNGCHELYIDAE developed by Hirayama et al. (2001) is the basis for this analysis, but the character matrix was subjected to minor changes. In particular, additional states were added to characters 18 and 24 (17 and 20 of

Hirayama et al., 2001), and characters 25, 26, and 32 of Hirayama et al. (2001) were split into separate characters (characters 26–29, 33, and 35) to encompass greater morphological variation. In contrast, character 16 is a hybrid of characters 22 and 24 of Hirayama et al. (2001), as the original character definitions are redundant. A list of modified character definitions is provided in appendix 1.

Four new characters were added to the analysis (6, 17, 35, 40) and two were removed from the analysis. Character 8 of Hirayama et al. (2001) refers to the amount of ossification that the canal for the carotid artery exhibits posterior to the junction with the palatine artery. Because of the poor preservation of the NANHSIUNGCHELYID skull material, we are not confident in scoring the presence or absence of this character from the literature. Omission of this character fortunately has no impact on the analysis, because the derived condition is purported as present only in *Nanhsiungchelys wuchingensis* (Hirayama et al., 2001).

According to character 16 of Hirayama et al. (2001), a unique sculpturing of the shell unites all members of the NANHSIUNGCHELYIDAE into a monophyletic group. Indeed, the shells of all ingroup turtles are characterized by sculpturing, but the morphology of these sculptures ranges from fine grooves and crenulations (e.g., *Anomalochelys angulata*) to uneven pits and pock-marks (e.g., *Basilemys variolosa*, *Zangerlia testudinimorpha*), making it difficult to objectively compare or homologize them. Given that the character is uninformative as currently presented, and that the outgroup *Adocus* sp. is also characterized by sculpturing, we omitted it.

Finally, the codings of characters 2–5, 8, 12, 13, 20, 21, 23, 26, and 28 of Hirayama et al. (2001) were reversed. This adjustment is purely cosmetic and was only undertaken to evenly render all primitive characters displayed in the outgroup *Adocus* sp. as ‘‘0’’ and all derived characters as ‘‘1’’ or ‘‘2’’.

The final data matrix includes 39 osteological characters and one geographical character with 44 derived character states for 10 representatives of NANHSIUNGCHELYIDAE and the outgroup *Adocus* sp. Including geography, this matrix only includes 18 informative characters with 22 derived character states, primarily due to significant amounts of missing data to the cranial region of most currently known NANHSIUNGCHELYIDS. The data matrix was assembled using McClade 3.08 (Maddison and Maddison, 1999) and analyzed using PAUP 4.0b10 (Swofford, 2002). Four phylogenetic analyses were performed that differ in their inclusion of the geographical character and in the ordering of the four multistate characters. Characters were considered reversible and of equal weight in all analyses. Under parsimony settings, branches were set to be collapsed if their minimum length was zero. Bootstrap values were calculated using PAUP 4.0b10. See appendices 1 and 2 for a complete list of characters used and the taxonomic distribution of character states.

PHYLOGENETIC NOMENCLATURE

NANHSIUNGCHELYIDAE, Converted Clade Name

DEFINITION: ‘‘NANHSIUNGCHELYIDAE’’ refers to the most inclusive clade containing *Nanhsiungchelys wuchingensis* Yeh, 1966, but not *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865) or any species of Recent turtle.

DISCUSSION: The name Nanhsiungchelyidae was originally coined by Yeh (1966), but he only referred *Nanhsiungchelys wuchingensis* to its content. It is current taxonomic practice to assign all turtles to the taxon Nanhsiungchelyidae that are hypothesized to be more closely related to *Nanhsiungchelys wuchingensis* than any species of *Adocus* (e.g., Brinkman and Peng, 1996; Sukhanov, 2000; Hirayama et al., 2001). We fix this relationship by tying the name ‘‘NANHSIUNGCHELYIDAE’’ to the most inclusive clade of turtles that contains *Nanhsiungchelys wuchingensis* but not *Adocus beatus*.

HYPOTHESIZED CONTENT: NANHSIUNGCHELYIDAE is hypothesized to contain the following taxa: *Nanhsiungchelys wuchingensis* Yeh, 1966, *Anomalochelys angulata* Hirayama et al., 2001, *Basilemys* (orig. *Compsemys*) *variolosa* (Cope, 1876), *B. nobilis* Hay, 1911, *B. sinuosa* Riggs, 1906, *B. praeclara* Hay, 1911, ‘‘*Basilemys*’’ *orientalis* Sukhanov and Narmandakh, 1977, *Zangerlia testudinimorpha* Mlynarski, 1972, *Z. neimongolensis* Brinkman and Peng, 1996, and *Z. ukhaachelys*, n.sp.

ADOCIDAE, Converted Clade Name

DEFINITION: ''ADOCIDAE'' refers to the most inclusive clade containing *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865) but not *Nanhsiungchelys wuchingensis* Yeh, 1966 or any species of Recent turtle.

DISCUSSION: The name Adocidae was originally coined by Cope (1870), but he only referred all species then thought to be included in the genus *Adocus*. In the last 20 years, the referred content of Adocidae has varied markedly (e.g., Mlynarski, 1976; Gaffney and Meylan, 1988; Sukhanov, 2000), but all of these usages overlap in the exclusion of *Nanhsiungchelys wuchingensis*. Consequently, we tie the name ''ADOCIDAE'' to the most inclusive clade of turtles that contains *Adocus beatus* but not *Nanhsiungchelys wuchingensis*.

HYPOTHESIZED CONTENT: Estimating the hypothesized content of ADOCIDAE is currently highly speculative because a phylogenetic analysis is not available. Likely candidates, however, include some North American taxa placed in the North American genus *Adocus* (see Hay, 1908) and numerous taxa placed in the Asian genera *Adocoides* and *Ferganemys* (see Sukhanov, 2000).

SYSTEMATIC PALEONTOLOGY

TESTUDINES BATSCH, 1788

CRYPTODIRA COPE, 1868

NANHSIUNGCHELYIDAE YEH, 1966

Zangerlia ukhaachelys, new species

HOLOTYPE: IGM 90/1 (figs. 1–4), incomplete skeleton consisting of partial cranium, peripherals, plastron, and fragmentary other remains of the postcranium.

TYPE LOCALITY: Ukhaa Tolgod, just south of Xanadu, Omongov Aimag, Mongolia. The Ukhaa Tolgod beds have been considered to be roughly equivalent to Djadoktha (Loope et al., 1998; Dashzeveg et al., 1995). Djadoktha beds elsewhere in Mongolia are considered to be Late Campanian (Lillegraven and McKenna, 1986; Gao and Norell, 2000).

ETYMOLOGY: ''Ukhaa'', in reference to the fossil locality Ukhaa Tolgod, Mongolia, and ''chelys'', Greek for turtle.

DIAGNOSIS: *Zangerlia ukhaachelys* is diagnosed by a single autapomorphy, the presence of an anteromedial process of the hyoplastron that limits contact between the entoplastron and epiplastron. In addition, *Zangerlia ukhaachelys* is diagnosed by the following list of synapomorphies and symplesiomorphies: cranium with enlarged nasal cavity; wide fissura ethmoidalis; well-developed upper temporal emargination; frontals do not contribute to orbit and produce descending processes that almost surround sulcus olfactorius ventrally; lingual ridges absent; antorbital groove present along anteroventral rim of orbit; shell covered with deep pock-marks, deep nuchal notch formed by small and trapezoid nuchal and first peripheral; vertebral and pleural scutes do not overlap onto peripherals; entoplastron dissected by humero-pectoral sulcus; four pairs of inframarginals present which fully separate marginals from plastral scutes; marginal VI not expanded ventromedially; pectoral does not contribute to axillary notch; midline plastral sulci straight.

DESCRIPTION AND COMPARISON OF IGM 90/1

PRESERVATION

Unlike many other fossils from the locality of Ukhaa Tolgod, IGM 90/1 is only moderately well preserved and shows signs of pre- or postdepositional decay due to scavenging and/or postburial insect activity. Most limb elements are absent, and only fragmentary remains of the girdles were found within the shell. No traces of vertebral column elements, including the neural elements of the carapace, are present. Despite the lack of these elements, parts of the skull remain intact and display details in morphology never seen before in a nanhsiungchelyid turtle. The skull was found within the carapace just above the entoplastron. This position, however, is not considered positive evidence for full neck retraction in NANHSIUNGCHELYIDAE, but may be coincidental, because the cranium is not in articulation with the neck and may have been moved before final deposition.

The shell is incompletely preserved and many areas that are useful in diagnosing NANHSIUNGCHELYID species are missing. Only the anterior and lateral peripherals remain of the carapace, thus obscuring the morphology

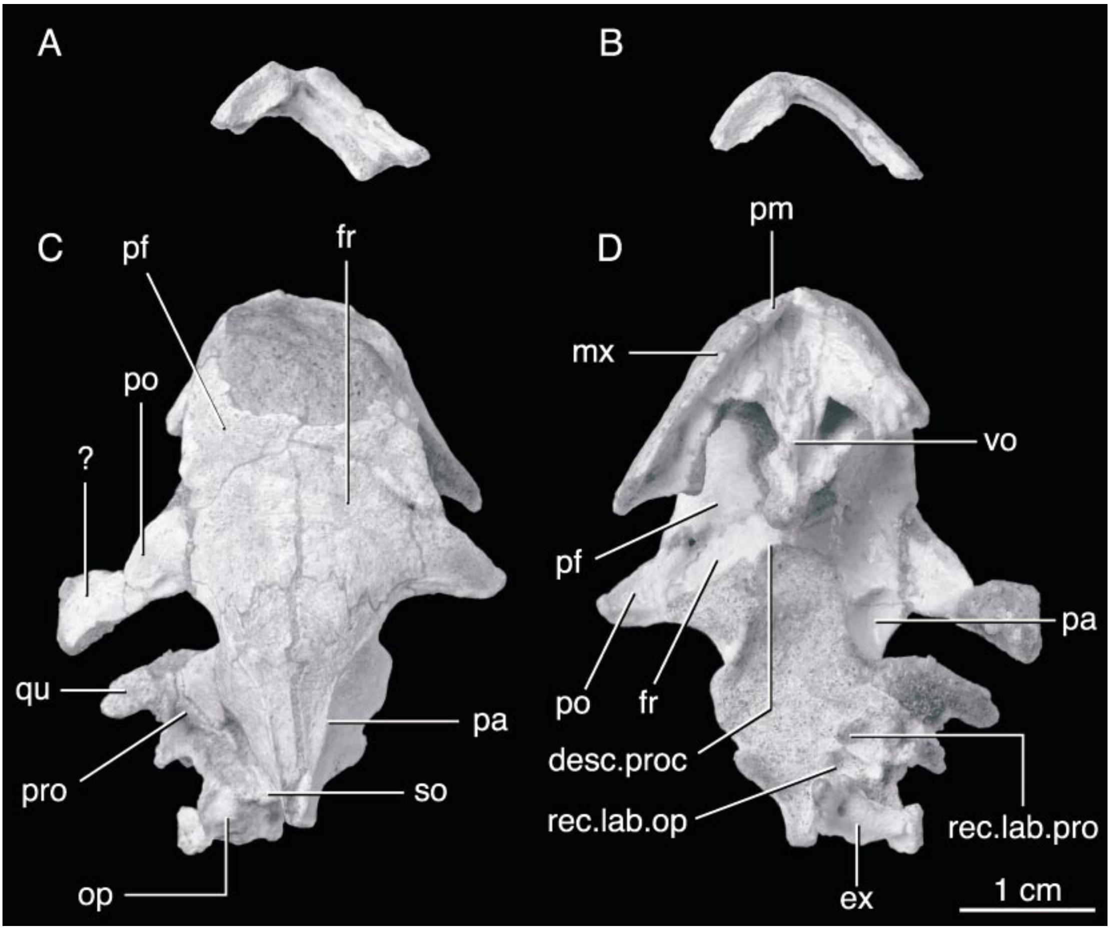


Fig. 1. *Zangerlia ukhaachelys*. IGM 90/1, holotype, Upper Cretaceous of Mongolia. Photographs were manipulated digitally to enhance sutures. **A,** Oblique dorsal view of mandible; **B,** dorsal view of mandible; **C,** dorsal view of cranium; **D,** ventral view of cranium. Abbreviations: **desc proc,** descending process of frontal; **ex,** exoccipital; **fr,** frontal; **mx,** maxilla; **op,** opisthotic; **pa,** parietal; **pf,** prefrontal; **pm,** premaxilla; **po,** postorbital; **pro,** prootic; **qu,** quadrate; **rec lab op,** recessus labyrinthicus opisthoticus; **rec lab pro,** recessus labyrinthicus prooticus; **so,** supraoccipital; **vo,** vomer; ?, bone of uncertain homology.

of most carapacial scutes and the nuchal and pygal region. The plastron is more complete, but significant parts of the anterior lobe and the bridges are missing or they are heavily weathered. The larvae of large scavenging beetles likely produced the holes seen in the plastron (figs. 1–4).

CRANIUM AND MANDIBLE

The most interesting aspect of IGM 90/1 is its uncrushed, partial cranium, which is the best preserved of any nanhsiungchelyid and clearly exhibits all cranial sutures (figs. 1, 2).

PREFRONTAL: The prefrontal of IGM 90/1 consists of a dorsal plate, which forms the roof of a broad fossa nasalis, and a vertical plate, which forms significant portions of the anterior orbit wall. In dorsal view, the prefrontal has a posteromedial contact with the frontal, a medial contact with its counterpart, and a small posterolateral contact with the postorbital, thus excluding the frontal from contributing to the orbital rim. The anterior rims of both prefrontals are weathered away, making it unclear if nasals were present anteriorly. In lateral view, the vertical plate of

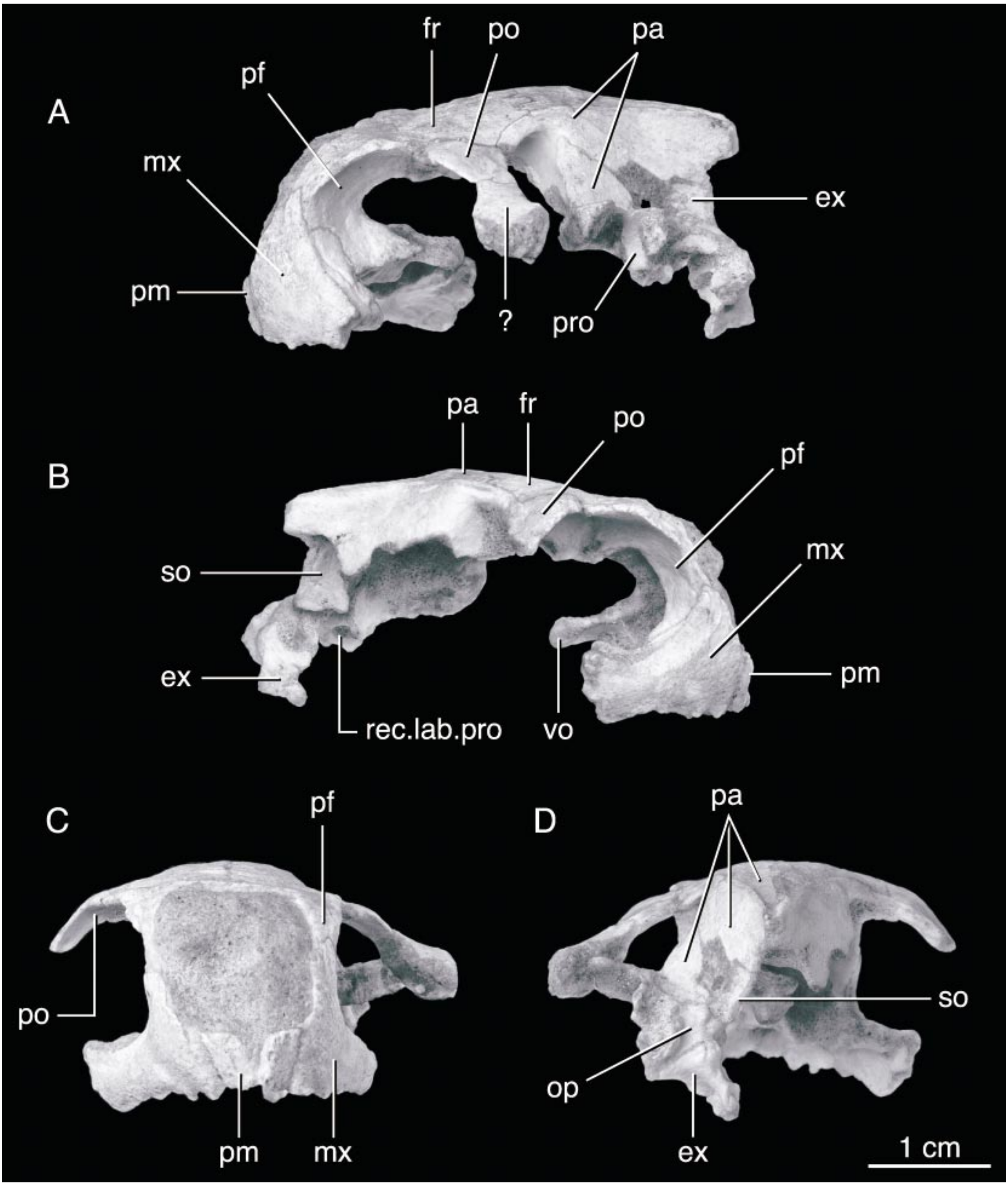


Fig. 2. *Zangerlia ukhaachelys*, cranium of IGM 90/1, holotype, Upper Cretaceous of Mongolia. Photographs were manipulated digitally to enhance sutures. **A,** Left lateral view; **B,** right lateral view; **C,** frontal view; **D,** caudal view. See figure 1 for abbreviations.

the prefrontal meets the ascending process of the maxilla along a short interdigitated contact to form the lateral wall of the fossa nasalis. An additional, elongate contact between these bones exists along the anteroventral rim of the orbit. Although the distal ends of the ascending process of the prefrontals are weathered, the left one is better preserved and shows the presence of a moderately sized foramen orbito-nasale. The fissura ethmoidalis and the sulcus olfactorius are apparent and are notably wide.

The prefrontal of IGM 90/1 closely resembles that of *Zangerlia neimongolensis*. It also resembles the prefrontals of *Adocus* sp., but differs by having a contact with the postorbital and by covering a much larger proportion of the dorsal roofing of the skull between the orbits. The fissura ethmoidalis greatly resembles that of the TESTUDINIDAE in being wide and not keyhole-shaped.

FRONTAL: In dorsal view, the frontal of IGM 90/1 is flat and subtriangular. It meets the prefrontal anterolaterally, the postorbital laterally, the other frontal medially, and the parietal along an interdigitated suture posteriorly. It is a large element forming much of the skull roof, but it does not contribute to the orbital rim. The frontal generally has a smooth surface, but a faint sulcus crosses it in an arch. The morphology of the frontal is more complex in ventral view. Between the parietal and the prefrontal, it forms a significant portion of the sulcus olfactorius. From the rim of the sulcus, tapered processes ascend from both frontals that almost meet medially, practically rendering the sulcus olfactorius a canal. Transverse to the sulcus olfactorius, the prefrontal additionally forms a small ridge that runs parallel to its border with the parietal and forms the posterodorsal limit of the orbit.

The skull materials of *Z. neimongolensis* and *N. wuchingensis* are not prepared enough to assess the presence of a descending frontal process in these taxa. These processes are not known in *Adocus* sp. Among living turtles, descending frontal processes are known from a number of TESTUDINOID turtles, especially terrestrial forms of the TESTUDINIDAE. The frontals of *Z. neimongolensis* do not contribute to the orbital rim, as seen in IGM 90/1. In contrast, the fronts of *Adocus* sp. and *N. wuchingensis* clearly do so.

PARIETAL: The parietals are partially preserved in IGM 90/1. Due to the great expanse of the prefrontal and frontal, this bone contributes very little to the dorsal surface of the skull between the upper temporal emarginations. It contacts the frontal anteriorly along an interdigitated transverse suture, meets its counterpart medially, and sends a small process anterolaterally along the rim of the upper temporal emargination to contact a similar postorbital process. No contacts are present with the jugal, quadratojugal, or squamosal because of the presence of a well-developed upper temporal emargination. Posteriorly, the parietal narrows to form the anterior part of the crista, but the posterior tip that overlies the supraoccipital is missing. The ventral portion of the parietal is less complete, but it appears to have formed much of the dorsal aspect of the lateral braincase wall, as in all crown group turtles. The parietal of IGM 90/1 appears to have contributed a little to a distinctly protruding processus trochlearis oticum.

The parietal of IGM 90/1 resembles that of *Adocus* sp., but it differs by contributing less to the skull roof and by having a small contact with the postorbital. The contacts of the parietal are unknown for *Z. neimongolensis*. The parietal of *N. wuchingensis* differs markedly by roofing much of the upper temporal fossa and by having contact with the squamosal.

POSTORBITAL: The postorbital is a small element that forms most of the slim postorbital bar. It contacts the prefrontal anteromedially and the parietal posteromedially, thus excluding the frontal from the orbit and the upper temporal emargination. It also contacts an element laterally, but the condition of the skull does not permit the identification of this bone as the jugal or quadratojugal.

PREMAXILLA: The premaxilla of IGM 90/1 is a small element that meets the maxilla laterally, its counterpart medially, and the vomer posteriorly and that forms the ventral rim of the external nares. Together with the maxilla, it forms a distinct, evenly serrated labial ridge. In ventral view, the premaxillae form the anterior portion of the narrow triturating surface. The position of the foramen praepalatinum is unclear. No significant differences are apparent from the premaxilla of *Adocus* sp. or *Z. neimongolensis*. Although the premaxilla was neither explicitly mentioned nor depicted by Yeh (1966) for *N. wuchingensis*, it must have deviated from the morphology of IGM 90/1 greatly, because the entire nasal region of this taxon protrudes to form a tubular snout.

MAXILLA: Both maxillae of IGM 90/1 are present, but only the right one is well preserved. This bone contacts the premaxilla anteriorly, the prefrontal dorsally and along the anteroventral rim of the orbit, and the vomer along a small suture posteromedially. It is likely that it contacts the jugal, pterygoid, and palatine; however, this cannot be directly observed in this specimen. The maxilla forms the vast majority of the coarsely serrated labial ridge in ventral view. A lingual ridge is absent, and the triturating surface is rather narrow and only slightly sculpted. In lateral view, an antorbital groove is apparent that lies parallel to the anteroventral rim of the orbit.

The maxilla of IGM 90/1 generally resembles that of *Adocus* sp. and *Z. neimongolensis*, but *Adocus* sp. is lacking the antorbital groove. The shape of the maxilla of *N. wuchingensis* has little resemblance to that of IGM 90/1.

VOMER: Only the anterior portion of the vomer is preserved. As in most CRYPTODIRES, it contacts the maxilla anterolaterally and the premaxilla anteromedially and separates the internal narial openings. The position of the praepalatine foramen is not clear. No discrete differences are apparent with *Adocus* sp. and *Z. neimongolensis*.

BRAINCASE ELEMENTS: Fragments of the left supraoccipital, prootic, opisthotic, exoccipital, and quadrate are preserved in IGM 90/1. Only the anterior portion of the supraoccipital remains to form the lateral braincase wall and the lateral rim of the foramen magnum. It is predominantly in contact with the parietal anteriorly and medially and with the opisthotic laterally. The processus trochlearis oticum is not distinct and appears to be predominantly formed by the parietal and quadrate. The prootic contributed to this structure with a minor sliver only. The anteromedial portions of the opisthotic are preserved, but the entire paroccipital process is missing. Together with the prootic, it forms a parasagittal groove within the upper temporal fossa. In ventral view, a number of internal structures are apparent, such as the recessus labyrinthicus prooticus and opisthoticus, but the specimen is too fragile to allow further preparation of this area. A small fragment of the exoccipital remains posterior to the opisthotic, but only the hypoglossal nerve foramina are apparent.

DENTARY: Only the anterior portions of both mandibular rami remain in IGM 90/1. The dentary is a narrow element that meets its counterpart along a narrow suture medially. The labial ridge is very low in what remains, and a modest triturating surface is present that overhangs the medial interdentary suture.

CARAPACE

Only some peripherals remain of the carapace. On the left side, peripherals I–V are preserved in articulation. The most anterior peripheral is identifiable as peripheral I, because it forms the apex of a deep nuchal notch. Such nuchal notches are typical of NANHSIUNGCHELYIDAE and are always formed by the nuchal and the first peripheral. Although the nuchal is missing in IGM 90/1, it can be inferred to have been small, similar to that found in ''*Basilemys*'' *orientalis*. Peripheral III, IV, and V loosely articulate with the hyoplastron. On the right side, the anterior element can be identified as peripheral III, based on its articulation with the hyoplastron, followed by peripherals IV, V, and VII–X.

Peripheral I is a pentagonal element. Its anterolateral side forms the carapace margin, and the anteromedial side forms the deep nuchal notch. Peripheral II is rectangular and almost twice as wide as long. Peripherals II–IX are bridge peripherals. The anterior three bridge elements are in contact with the hyoplastron, and the posterior four are in contact with the hypoplastron. The angle that is formed between the dorsal and ventral plates of these peripherals is approximately 90°. In life, the actual angle of the carapace, however, was probably only 50°. All elements have clear traces of marginal scutes. The pleural and vertebral scutes did not reach the peripherals.

PLASTRON

The plastron of IGM 90/1 is well preserved, although significant portions of the anterior plastral lobe and the bridges are missing (figs. 3, 4). An elongate central fontanelle and two small, semilunate lateral fontanelles are formed by the hyo- and hypoplastra. Central fontanelles are also known from *Zangerlia neimongolensis*. Most sulci can be clearly traced, but due to the poor preservation of the anterior bony elements, there is no evidence of gulars and extragulars. All plastral elements are ornamented with irregular grooves and pits, a feature characteristic of many TRIONYCHOIDS. All bony sutures can be traced easily, because the bones only contact each other bluntly, thus allowing the elements to separate after death. Given the significantly smaller size of IGM 90/1 relative to other members of the NANHSIUNGCHELYIDAE, this weak development of the bony contacts together with the lateral fontanelles may represent juvenile features.

ANTERIOR PLASTRAL ELEMENTS: Although much of the anterior plastron lobe is missing or detached, it is apparent that this lobe was rather well developed, probably reaching farther anteriorly than the carapace rim. This feature is typical for NANHSIUNGCHELYID turtles. The entoplastron is a large, diamond-shaped element that is fully surrounded by the epiplastra anteriorly and thus is excluded from the plastral rim. A unique characteristic of IGM 90/1 is the arrangement of contacts between the entoplastron, epiplastron, and hyoplastron. In all crown group turtles with a well-ossified plastron, including *Adocus* and all representative of NANHSIUNGCHELYIDAE, the entoplastron is a diamond-shaped element that only contacts the epiplastron along its anterolateral side. In IGM 90/1, the hyoplastron sends a triangular process anterolaterally that separates the epiplastron from the entoplastron, thus limiting the contact that usually exists between these two elements. Although this morphology is only clearly seen on the left side and may be considered an anomaly, there is no trace of a suture at its regular position on the right side, confirming the fidelity of the morphology depicted on the left. Detached remains of the epiplastra indicate that the anterior rim of the plastron was rounded and that the gular scute extended onto a thickened dorsal lip.

BRIDGE REGION: The bridge of IGM 90/1 is formed by the hyoplastron and hypoplastron. Mesoplastra are absent. Anterior and posterior plastral buttresses are present but are only poorly developed, as in all NANHSIUNGCHELYID turtles. The anterior plastral buttress reaches to contact the third peripheral, and the posterior buttress just barely appears to contact the ninth peripheral. Distally, the buttresses flare into numerous fingers, which established a loose, sutural connection between the carapace and the plastron. The axillary notch is positioned just slightly farther anteriorly than the posterior end of the entoplastron and the inguinal notch just slightly anterior to the hypo/xiphiplastral suture.

POSTERIOR PLASTRAL ELEMENTS: The posterior plastral lobe is formed predominantly by the xiphiplastron. This is typical for NANHSIUNGCHELYIDAE. Like most turtles, the suture between the hypoplastron and xiphiplastron is generally straight but is Z-shaped near the lateral rim.

PLASTRAL SCUTES: No clear traces of the gulars and extragulars can be found. This is unfortunate, as many diagnostic features of NANHSIUNGCHELYIDAE can be found in this region. Similar to *Zangerlia neimongolensis*, the humero-pectoral sulcus clearly intersects the entoplastron medially, but it is unclear where this sulcus terminates laterally. As in all NANHSIUNGCHELYID turtles, the pectoral increases in length medially, but its midline sulcus appears to be straight, unlike in *Basilemys* spp. The lateral contacts of the pectoral are unclear, but the pectoral appears to widen slightly to contact the first two inframarginals. The pectoral does not contribute to the anterior plastral rim. The abdominal is a subrectangular element, with the exception of a small posterolateral process that contributes to the rim of the inguinal notch and hinders contact between the femoral and the posterior inframarginal. The anal is a triangular element and its medial contact is straight, as in *Z. testudinimorpha*.

IGM 90/1 has a complete row of four in-

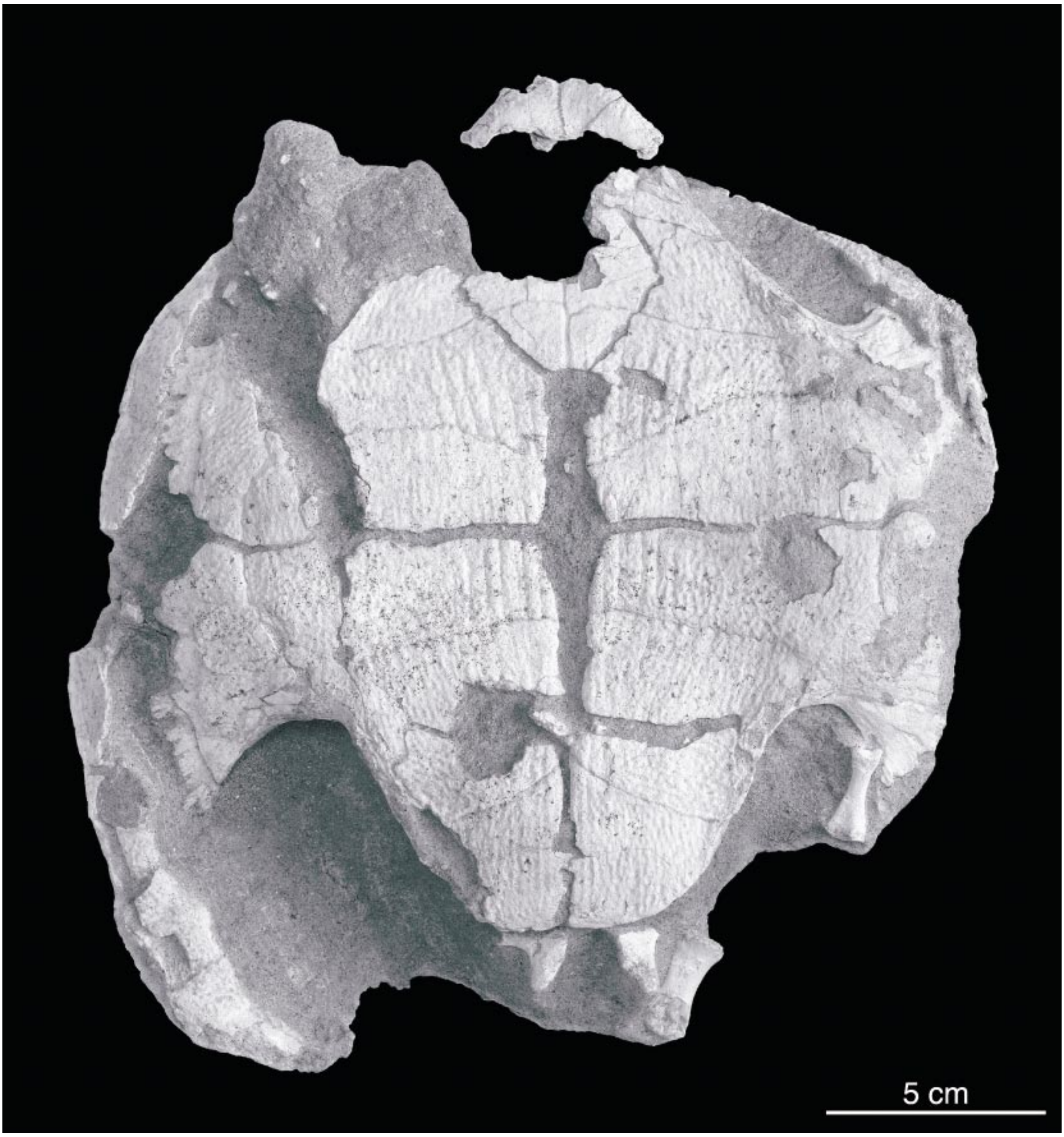


Fig. 3. *Zangerlia ukhaachelys*, IGM 90/1, holotype, Upper Cretaceous of Mongolia. Ventral view of plastron.

framarginals. The anterior inframarginal is the least well preserved. Only its posterior sulcus with the second inframarginal is clearly visible. The second inframarginal is a pentagonal element that has a straight lateral contact with the marginals, a straight anterior contact with the first inframarginal, and a straight posterior contact with the third inframarginal. It meets the pectoral anteromedially and the abdominal posteromedially. The third inframarginal is an elongate, rectangular element and spans the hyo-/hypoplastral suture. It is subequal in length with the other inframarginals. The posterior inframarginal is less visible, but it appears to become significantly wider posteriorly. The marginals clearly overlap onto the plastron, but no intermarginal sulci are apparent on the ventral

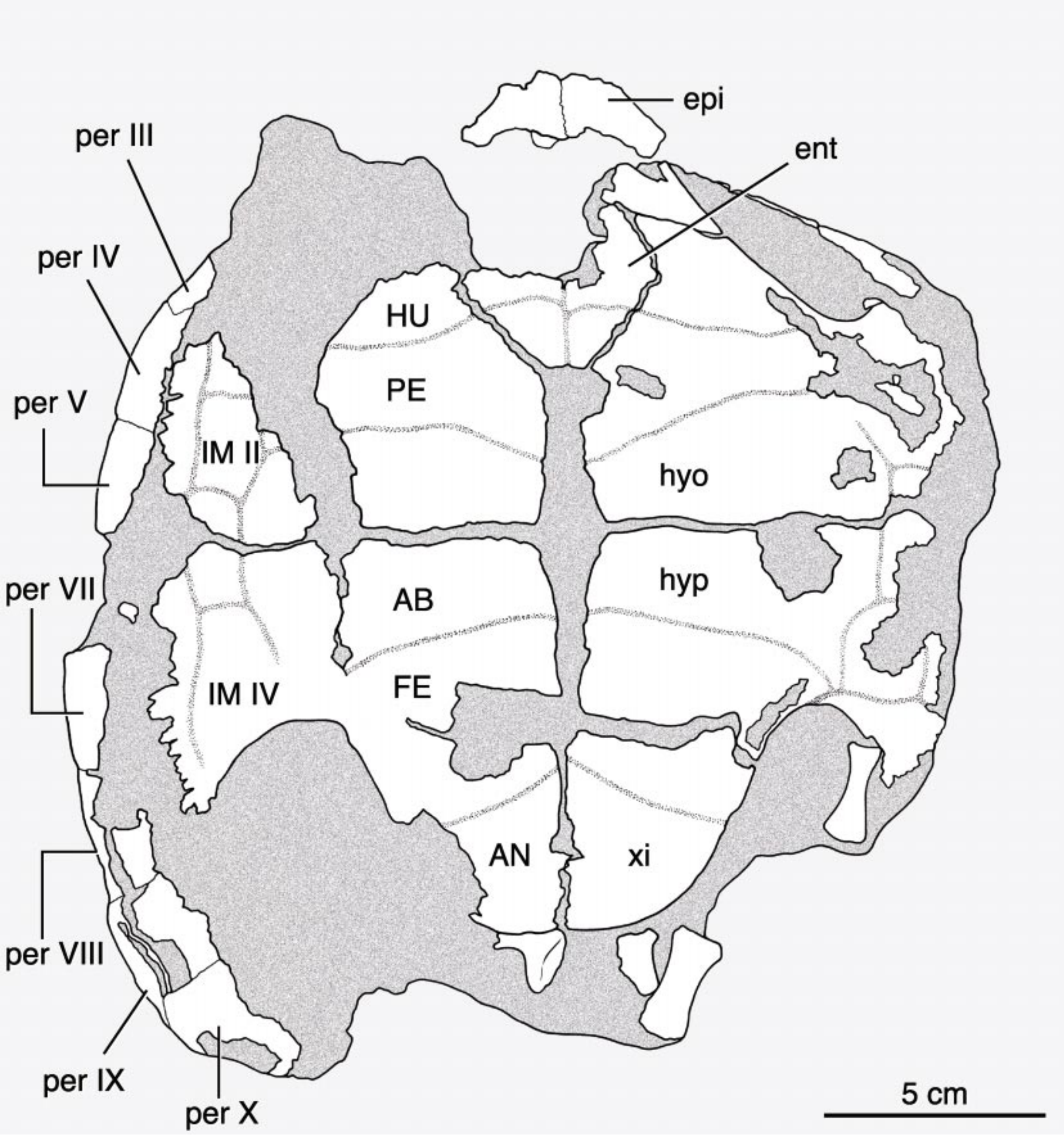


Fig. 4. *Zangerlia ukhaachelys*, IGM 90/1, holotype, Upper Cretaceous of Mongolia. Ventral view of plastron. Abbreviations: **AB,** abdominal scute; **AN,** anal scute; **ent,** entoplastron; **epi,** epiplastron; **FE,** femoral scute; **HU,** humeral scute; **hyo,** hyoplastron; **hyp,** hypoplastron; **IM,** inframarginal scute; **PE,** pectoral scute; **per,** peripheral; **xi,** xiphiplastron.

side. A row of four equally sized inframarginals is unique among NANHSIUNGCHELYIDS. ''*Basilemys*'' *orientalis* also has a complete row of inframarginals, but the third inframarginal is at least three times longer than the other elements. The inframarginals of *Zangerlia* spp. and *Basilemys* spp. are reduced both in number and in size.

POSTCRANIAL ELEMENTS

Few postcranial elements were found associated with IGM 90/1. Additional elements may be hidden in the remaining matrix; however, further preparation was not undertaken to avoid destabilizing the plastron.

SCAPULA: The scapular process is exposed in dorsal view, but the remaining parts of the scapula are still covered by sediments. The scapular process is flattened in cross section, its shaft is striated, and it is curved. From what can be seen, this element greatly resembles the scapula of *Zangerlia neimongolensis*.

SACRAL RIBS: Two sacral ribs are preserved just posterior to the plastron (figs. 3, 4). Like the sacral ribs of most CRYPTODIRES, these elements are narrow distally for articulation with the ilium, but they expand proximally for articulation with the sacral vertebrae. Unlike those of other CRYPTODIRES, the sacral ribs of *Zangerlia ukhaachelys* are approximately five times wider proximally than distally, and the proximal end is flattened, not cylindrical. Comparative material is not available from other NANHSIUNGCHELYIDS.

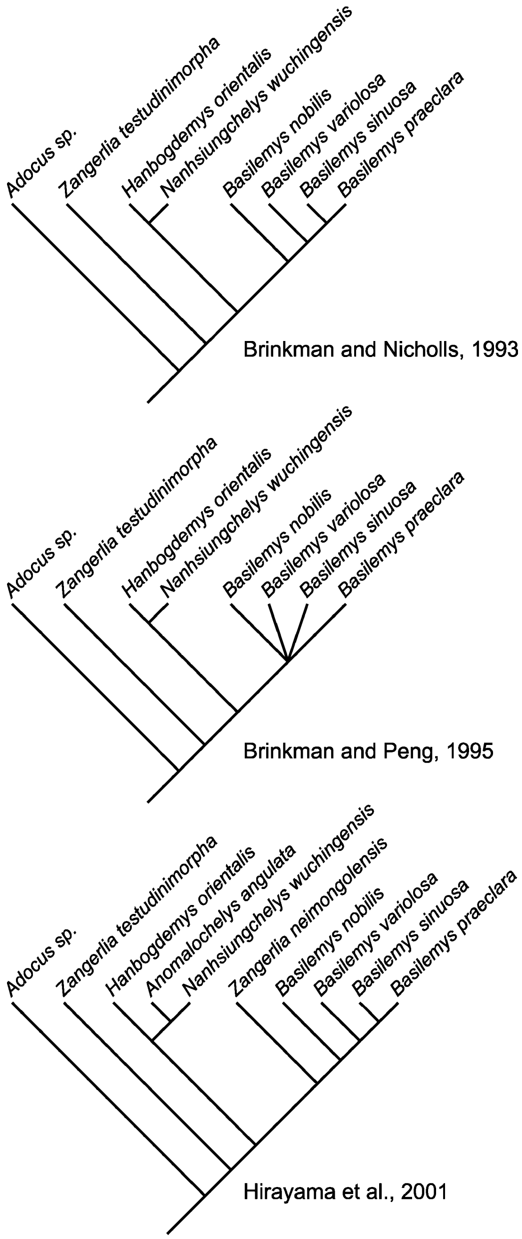
ILIUM AND TIBIA: A single, partially crushed element is present in close association with the sacral ribs that is tentatively interpreted as the ilium (figs. 3, 4). This identification is supported by a slight distal expansion to the bone and the presence of three facets proximally that may correspond to the articular sites with the pubis and ischium and the acetabulum. Adjacent to the left inguinal buttress another bone is preserved which appears to be a tibia. Both elements are unusually short relative to the length of the carapace, however, making this identification somewhat uncertain. Additional material of *Zangerlia ukhaachelys* will certainly help reveal the identity of these elements.

DISCUSSION

IGM 90/1 exhibits a number of characteristics of the NANHSIUNGCHELYIDAE that help distinguish it from all other turtles. These include the antorbital groove of the maxilla, the short limbs, the well-developed anterior plastral lobe, a thickened epiplastral lip, and the absence of a pectoral contribution to the axillary rim. Unlike all representatives of the North America *Basilemys*, IGM 90/1 is characterized by a full set of four inframarginals and the complete absence of an overlap of the pleural and vertebral scutes onto the peripherals and the pygal. Although the nuchal is not present in IGM 90/1, it can be clearly inferred not to have been a large V-shaped element as seen in *Anomalochelys angulata* or *Nanhsiungchelys wuchingensis*, because the adjacent first peripheral closely approached the midline not allowing room for a large nuchal. IGM 90/1 differs from ''*Basilemys*'' *orientalis* by possessing subequally sized inframarginals and by lacking a sinuous interanal sulcus and a ventromedially expanded sixth marginal. Within *Zangerlia*, IGM 90/1 differs from *Z. neimongolensis* and *Z. testudinimorpha* by its complete row of four subequally sized inframarginals. Most importantly, IGM 90/1 can be differentiated from all other representatives of *Zangerlia* and all turtles in general by the development of an anteromedial process of the hyoplastron that hinders a full contact between the anterolateral side of the entoplastron with the epiplastron. These differences, especially the arrangement of bones in the anterior plastral lobe, clearly diagnose IGM 90/1 as a new species, which we name *Zangerlia ukhaachelys* in reference to the type locality, Ukhaa Tolgod, Mongolia.

PHYLOGENETIC RELATIONSHIPS

The assemblage of turtles currently hypothesized to belong to NANHSIUNGCHELYIDAE (i.e., *Basilemys variolosa*, ''*Basilemys*'' *orientalis*, *Nanhsiungchelys wuchingensis*, *Zangerlia testudinimorpha*) was formally recognized as a phylogenetic unit by Sukhanov and Narmandakh (1977), who placed all of these taxa into *Basilemys*. Subsequently, most authors have agreed that these turtles form a monophyletic group (e.g., Meylan and Gaffney, 1989; Brinkman and Peng, 1996; Sukhanov, 2000; Hirayama et al., 2001). The phylogenetic relationships within NANHSIUNGCHELYIDAE have only been scrutinized within a cladistic framework for the last 15 years. Notably, Meylan and Gaffney (1989) placed NANHSIUNGCHELYIDAE as the sister to *Peltochelys* and TRIONYCHIA within the TRIONYCHOIDEA, but they did not resolve internal relationships. Using the first species-level cladistic analysis, Brinkman and Nicholls (1993) demonstrated that *Zangerlia tes-*



Brinkman and Nicholls, 1993

Brinkman and Peng, 1995

Hirayama et al., 2001

Fig. 5. Previously published phylogenetic hypotheses of NANHSIUNGCHELYIDAE.

tudinimorpha should be regarded as the most basal member of NANHSIUNGCHELYIDAE and that the Asian taxa *Nanhsiungchelys wuchingensis* and “*Basilemys*” *orientalis* form the sister group to the North American representatives of *Basilemys* (fig. 5). In contrast, Brinkman and Peng (1996) considered *Nanhsiungchelys wuchingensis* and “*Basilemys*” *orientalis* to represent the most basal divergence, being the sister group to all remaining taxa (fig. 5). The recent analysis of Hirayama et al. (2001) is somewhat intermediate relative to the previous two by considering *Zangerlia* to be paraphyletic and by placing *Zangerlia testudinimorpha* basal to all other turtles (as suggested by Brinkman and Nicholls, 1993) and “*Zangerlia*” *neimongolensis* as sister to *Basilemys* (as suggested by Brinkman and Peng, 1996; fig. 5).

In this study, four analyses were performed that differ in their inclusion of the geographical character and the ordering of the four multistate characters. The resulting four strict consensus trees are given in figure 6. Consistency indices range from 0.84 to 0.86 or 0.72 to 0.76 after removal of uninformative characters.

All four analyses support a clade comprised of *Zangerlia ukhaachelys*, *Z. testudinimorpha*, and *Z. neimongolensis*, a clade comprised of *Nanhsiungchelys wuchingensis* and *Anomalochelys angulata*, and a clade that includes all herein mentioned species of North American *Basilemys*. Bootstrap values provide good support for the clade comprised of *Nanhsiungchelys wuchingensis* and *Anomalochelys angulata*, and modest support for the clades comprised of all representatives of *Zangerlia* and North American *Basilemys*, respectively.

Unlike the results of Hirayama et al. (2001), this analysis supports the monophyly of *Zangerlia*, regardless of the inclusion of geography or the ordering of the multistate characters. If *Zangerlia ukhaachelys* is omitted and the paraphyly of *Zangerlia* forced as seen in Hirayama et al. (2001), two more steps are required in the trees that exclude geography or three in those that include geography. The most parsimonious addition of *Zangerlia ukhaachelys* to these forced trees (as sister to *Zangerlia testudinimorpha* or *Zangerlia neimongolensis*) requires four or five more steps, respectively. The strongest evidence in favor of a monophyletic *Zangerlia*, therefore, is not provided by the revision of the character matrix, but rather by the addition of *Zangerlia ukhaachelys* to the matrix. Representatives of *Zangerlia* are united by the loss of the lingual ridge, the steep pos-

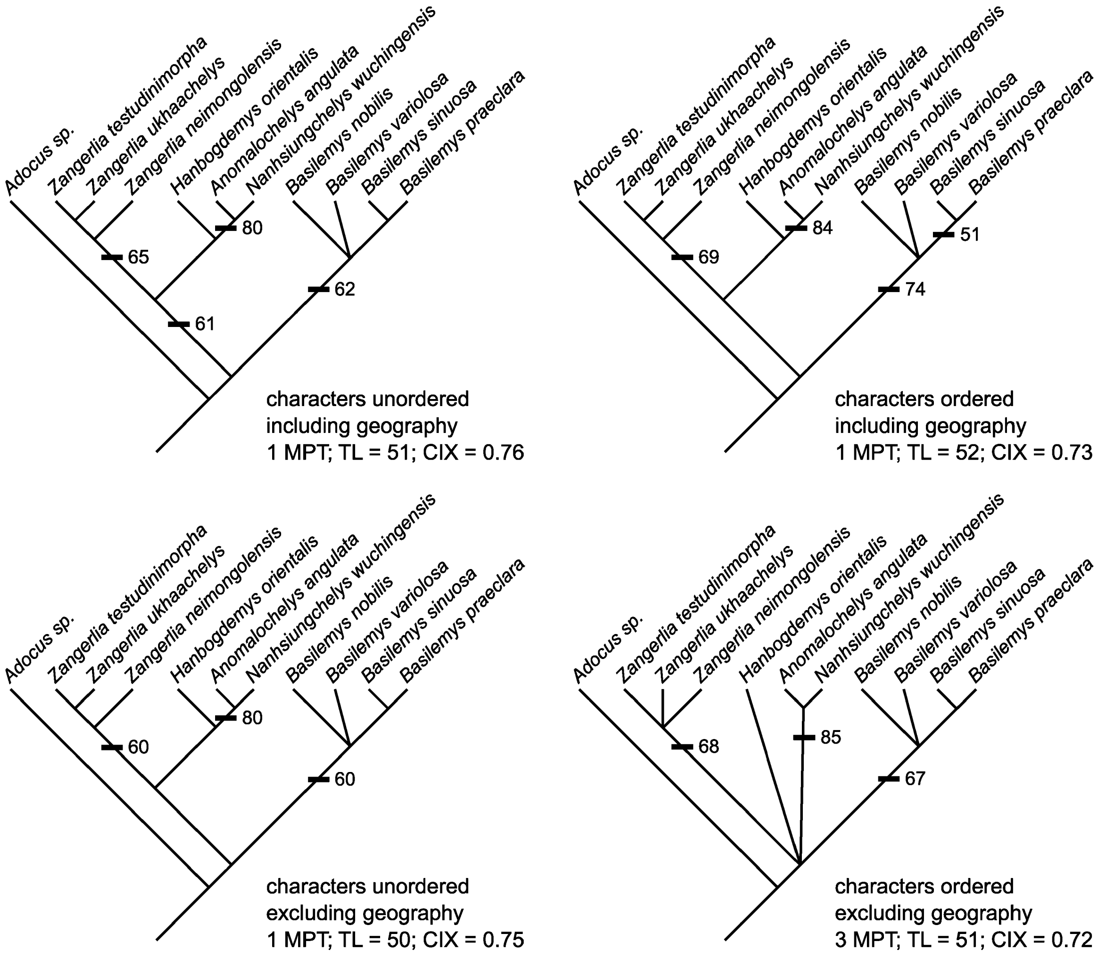


Fig. 6. Phylogenetic relationships of NANHSIUNGCHELYIDAE based on this analysis.

terior deflection of the carapace, and the presence of a knobby protrusion at the end of the neural series.

As in all previous studies, our analysis indicates the presence of a monophyletic clade of North American NANHSIUNGCHELYIDAE, termed *Basilemys*. Characters that unite this clade include the strong reduction of the inframarginals, which allows broad contact between the marginals and plastral scutes, and the broad overlap of the pleural and vertebral scutes onto the peripherals and pygal. The character that most clearly distinguishes these taxa from all other turtles is the broad overlap of a triangular fifth vertebral over the tenth peripheral.

In contrast to all previously published phylogenies, three out of four analyses retrieve a monophyletic clade of Asian NANHSIUNGCHELYIDS. This topology is not seen in the strict consensus cladogram of the analysis that includes ordering and excludes geography, but it is present in one of the three most parsimonious trees that this analysis provides. Characters that unite an Asian clade of NANHSIUNGCHELYIDAE include the correspondence of the pleural-marginal sulcus with the costal-peripherals suture and, most notably, the formation of a deep, triangular nuchal notch that is unique among turtles. Although we generally favor this topology, support for an Asian clade is limited. A paraphyletic assemblage of Asian NANHSIUNGCHELYIDS is retrieved in two of the three most parsimonious solutions in the analysis that excludes geography but includes ordered characters, and forcing paraphyly in the other analyses only results in trees one or two steps longer.

The occurrence of NANHSIUNGCHELYID and ADOCID turtles in North America and Asia only is evidence for the close biogeographic ties between these two landmasses during the Late Cretaceous. The presence of a monophyletic clade of North American NANHSIUNGCHELYIDS and an at worst paraphyletic assemblage of Asian NANHSIUNGCHELYIDS, however, illustrates that faunal exchange between these continents was limited, at least among these groups of turtles.

CONCLUSIONS

A fragmentary fossil turtle from the Late Cretaceous of Ukhaa Tolgod, Mongolia, is identified as a new species of NANHSIUNGCHELYID turtle, *Zangerlia ukhaachelys*. The most diagnostic trait that clearly distinguishes this taxon from all other known turtles is an anteromedial extension of the hyoplastron that hinders the usual broad anterolateral contact of the entoplastron with the epiplastron. In comparison with published accounts, phylogenetic analysis provides support for a clade comprised of *Zangerlia ukhaachelys*, *Z. neimongolensis*, and *Z. testudinimorpha*. Good support is present in favor of a clade containing *Anomalochelys angulata* and *Nanhsiungchelys wuchingensis* and a clade comprised of all North American representatives of *Basilemys*. Modest character support is also available for a clade that unites all Asian NANHSIUNGCHELYIDS. Biogeographic considerations indicate that the Late Cretaceous turtle faunas of Asia and North America are rather similar, but also that the amount of faunal exchange was very limited, at least within NANHSIUNGCHELYIDAE.

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APPENDIX 1

CHARACTER LIST

1. **Numerous deep cranial scute sulci on dermal roofing elements** (modified from Hirayama et al., 2001: char. 1: (0) absent; (1) present. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
2. **Extensive postorbital squamosal contact due to the great anterior extent of the squamosal and the great posterior extent of the postorbital** (modified from Hirayama et al., 2001: char. 2): (0) absent; (1) present. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
3. **Extent of upper temporal emargination** (Hirayama et al., 2001: char. 3): (0) foramen stapedio-temporale fully exposed in dorsal view; (1) foramen stapedio-temporale concealed in dorsal view. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
4. **Extent of lower temporal emargination** (Hirayama et al., 2001: char. 4): (0) moderately developed, processus pterygoideus externus barely visible in lateral view; (1) absent or shallow, processus pterygoideus externus concealed in lateral view. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
5. **Lingual ridges of maxilla** (Hirayama et al., 2001: char. 5): (0) double; (1) single or absent. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
6. **Antorbital groove on the surface of the maxilla along the anteroventral rim of the orbit**: (0) absent; (1) present.
7. **Medial contact of palatines** (Hirayama et al., 2001: char. 6): (0) absent; (1) present. COMMENTS: *Nanhsiungchelys wuchingensis* scored according to Hirayama et al. (2001).
8. **Incisura columella auris** (Hirayama et al., 2001: char. 7): (0) open posteriorly; (1) closed posteriorly. COMMENTS: *Basilemys variolosa* scored according to Hirayama et al. (2001).
9. **Size and contacts of the basisphenoid** (Hirayama et al., 2001: char. 9): (0) basisphenoid short, anteriorly only in contact with pterygoid; (1) basisphenoid elongate, anteriorly in contact with vomer or palatine. COMMENTS: *Nanhsiungchelys wuchingensis* scored according to Hirayama et al. (2001).
10. **Central morphology of the eighth cervical** (Hirayama et al., 2001: char. 10): (0) opistocoelous; (1) biconvex.
11. **Coracoid** (Hirayama et al., 2001: char. 11): (0) flat and elongate; (1) flat, fan-shaped. COMMENTS: *Basilemys variolosa* and ‘‘*Basilemys*’’ *orientalis* scored according to Hirayama et al. (2001).
12. **Size and medial contact of thyroid fenestrae** (Hirayama et al., 2001: char. 12): (0) fenestrae large and confluent; (1) fenestrae small, medial contact absent. COMMENTS: Scoring of *Zangerlia neimongolensis* changed from ‘‘1’’ to ‘‘0’’. *Basilemys variolosa* and ‘‘*Basilemys*’’ *orientalis* scored according to Hirayama et al. (2001).
13. **Thelial process of ilium** (Hirayama et al., 2001: char. 13): (0) present; (1) absent. COMMENTS: *Basilemys variolosa*, ‘‘*Basilemys*’’ *orientalis*, and *Nanhsiungchelys wuchingensis* scored according to Hirayama et al. (2001).
14. **Length of manual and pedal digits** (modified from Hirayama et al., 2001: char. 14): (0) digits elongate, typically three phalanges per digit; (1) digits shortened, less than three phalanges per digit. COMMENTS: *Basilemys variolosa*, *Basilemys nobilis*, and ‘‘*Basilemys*’’ *orientalis* scored according to Hirayama et al. (2001).
15. **Limb osteoderms** (Hirayama et al., 2001: char. 15): (0) absent; (1) present. COMMENTS: *Basilemys variolosa*, and *Basilemys nobilis* scored according to Hirayama et al. (2001).
16. **Steep deflection of the postneural part of the carapace** (Hirayama et al., 2001: chars. 22, 24): (0) absent, posterior peripherals great flared; (1) present, posterior peripherals shortened.
17. **Knobby protrusion of the carapace at the position of the first suprapygal**: (0) absent; (1) present.
18. **Nuchal notch** (modified from Brinkman and Nicholls, 1993: char. 2; Hirayama et al., 2001: char. 17): (0) absent or shallow; (1) present, formed by the nuchal and peripheral I; (2) present, formed by nuchal only. COMMENTS: Scoring of *Zangerlia testudinimorpha* changed from ‘‘0’’ to ‘‘?’’.
19. **Shape and size of nuchal** (Hirayama et al., 2001: char. 19): (0) small and trapezoid; (1) large and V-shaped.
20. **Costiform process of nuchal** (Hirayama et al., 2001: char. 18): (0) absent; (1) present.

COMMENTS: Scoring of *Zangerlia testudinimorpha* changed from ''1'' to ''?''.

21. **Neurals** (Hirayama et al., 2001: char. 21): (0) neurals VII and VIII reduced or lost; (1) full set of eight neurals present.
22. **Contacts of suprapygals with peripherals** (modified from Hirayama et al., 2001: char. 23): (0) contact with peripherals X and XI; (1) contact with peripheral XI only.
23. **Shape of pygal** (Brinkman and Nicholls, 1993: char. 4d): (0) longer than wide; (1) wider than long.
24. **Anterior contacts of vertebral I** (modified from Hirayama et al., 2001: char. 20): (0) anterior side very wide, in contact with marginal II; (1) anterior side moderately wide, in contact with marginal I; (2) anterior side constricted, primarily in contact with cervical only.
25. **Contacts of vertebral V with marginals X and XI** (modified from Hirayama et al., 2001: char. 27): (0) vertebral V only in contact with half the length of marginal XI; (1) vertebral V contacts full length of marginal XI and may even contact marginal X.
26. **Position of vertebral V relative to suprapygals** (modified from Hirayama et al., 2001: char. 26): (0) vertebral V only partially covers suprapygals; (1) vertebral V fully, or almost fully, covers the suprapygals.
27. **Position of vertebral V relative to peripheral X** (modified from Hirayama et al., 2001: char. 26): (0) vertebral V does not reach peripheral X; (1) vertebral V clearly covers part of peripheral X.
28. **Sulcus between pleural I and marginals II and III** (modified from Hirayama et al., 2001: char. 25): (0) clearly situated on peripherals; (1) situated on or near suture of peripherals and costals or clearly situated on costals.
29. **Sulcus between pleural III and marginals VII–IX** (modified from Hirayama et al., 2001: char. 25): (0) clearly situated on costals; (1) situated near suture of peripherals and costals; (2) clearly situated on peripherals.
30. **Extent of anterior plastral lobe** (Hirayama et al., 2001: char. 36): (0) anterior lobe covered by carapace in dorsal view; (1) anterior lobe protrudes farther anterior than carapace.
31. **Extragulars** (modified from Hirayama et al., 2001: char. 32): (0) present; (1) absent.
32. **Fusion of gulars** (Hirayama et al., 2001: char. 33): (0) absent; (1) present.
33. **Size and medial contact of extragulars** (modified from Brinkman and Nicholls, 1993: char. 4a; Hirayama et al., 2001: char. 32): (0) extragulars small or absent, and, if present, do not meet medially; (1) extragulars elongate, in medial contact with another, thus hindering a contact between gulars and humerals.
34. **Broad dorsal extension of gulars onto thickened anterior plastral lip** (Hirayama et al., 2001: char. 35): (0) absent; (1) present.
35. **Position of gulars and extragulars relative to entoplastron**: (0) scutes do not overlap entoplastron; (1) scutes overlap onto entoplastron.
36. **Humero-pectoral sulcus** (Hirayama et al., 2001: char. 34): (0) does not intersect entoplastron; (1) intersects entoplastron. COMMENTS: Scoring of *Zangerlia testudinimorpha* changed from ''1'' to ''0''.
37. **Inframarginals** (Hirayama et al., 2001: char. 29): (0) four or three pairs; (1) two pairs; (2) absent. COMMENTS: Scoring of *Zangerlia neimongolensis* changed from ''0/1'' to ''0''.
38. **Expansion of the ventromedial edge of marginal VI** (Brinkman and Nicholls, 1993: char. 1; Hirayama et al., 2001: char. 30): (0) absent; (1) present. COMMENTS: Scoring of *Basilemys praeclara* changed from ''1'' to ''?''.
39. **Participation of pectoral to rim of axillary notch** (modified from Hirayama et al., 2001: char. 31): (0) present; (1) absent.
40. **Geographical distribution**: (0) North America; (1) Asia.

APPENDIX 2

TAXON–CHARACTER MATRIX

	1		11		21		31	
Adocus sp.	00000	00000	00000	00000	00000	00000	00000	a0000
Zangerlia testudinimorpha	?????	?????	???1?	11?0?	11111	1011?	?????	000a1
Zangerlia neimongolensis	00001	1?101	?0111	11???	101?1	00?11	00111	10111
Zangerlia ukhaachelys	00001	1????	?????	1?10?	??1??	?0111	???1?	10011
Basilemys variolosa	00000	1?1??	11111	00000	10111	01021	00011	11110
Basilemys nobilis	?????	?????	???11	0000?	00111	01021	01011	11110
Basilemys sinuosa	?????	?????	?????	0000?	101a1	01021	00111	11110
Basilemys praeclara	?????	?????	?????	0??0?	??1?1	0102?	00111	1???0
“Basilemys” orientalis	?????	?????	1111?	00101	10110	00111	01010	10111
Anomalochelys angulata	?????	?????	?????	?0110	1??2?	???1?	01011	???11
Nanhsiungchelys wuchingensis	1111?	?111?	??111	?021?	1??21	??111	11011	12??1

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